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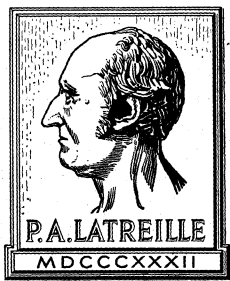
LIVRE
DU
CENTENAIRE

*Natura maxime miranda
in minimis.*

AN EXTRAORDINARY ANT-GUEST FROM THE PHILIPPINES

(*Aenictoteras Chapmani*, gen. et sp. nov.)

By W. M. WHELLER



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A LARGE number of myrmecophiles are known from colonies of the driver and legionary ants of the genera *Dorylus* and *Eciton*, but few have been recorded from colonies of the third large Doryline genus, *Aenictus*. The meager literature contains descriptions of only three aenictophilous Staphylinid beetles, namely, *Aenictonia cornigera* Wasmann (1900) of the Orange Free State, from a colony of *Aenictus eugenii* Emery, *Aenictonia hemigastrophysa* Eichelbaum (1913), associated with an East African species of *Aenictus*, and *Trilobitideus mirabilis* Raffray, occurring with the same host as *Aenictonia cornigera*. Recently BRUES (1930) has described a Phorid fly, *Diploneura* (*Aenictomyia*) *chapmani* taken by Dr. J. W. CHAPMAN with *Aenictus* (*Typhlatta*) *martini* Forel in the Philippines. With this same ant Dr. CHAPMAN also took several specimens of a highly aberrant Staphylinid, which is here described as the type of a new genus of *Aleocharinae* of the tribe *Myrmedoniini*.

Gen. AENICTOTERAS, nov.

Very slender; head somewhat flattened, subtrapezoidal, nearly one and a half time as long as broad, narrowed behind, truncated in front, with very feebly convex lateral and posterior borders, the anterior border two thirds broader than the posterior, rectangularly excised, with a prominent tooth at the inner corner of each of the lateral lobes thus formed. Eyes well-developed, subhemispherical and projecting, at the anterior corners of the head. Front subtriangular, broader than long, rounded behind, decidedly impressed. Antennae long, 11-jointed; first joint large, clavate, rather thick, three times as long as broad, as long as the combined second and third

joints which are slender and cylindrical, the second being distinctly longer than the third; joints 4-10 much shorter, subcylindrical, monillate, sharply marked off from one another; terminal joint thicker, as long as the two preceding joints together, its tip bluntly rounded. Mandibles falcate, with long, feebly curved tips, widened and bluntly subdentate near the middle. Gula long and narrow, with pronounced lateral sutures; mentum bilobed, with a median suture; ligula broader than long, with broadly and evenly rounded, entire anterior border. Maxillary palpi indistinctly 4-jointed, the two median joints stout, the terminal joint slender, styliform; maxillary

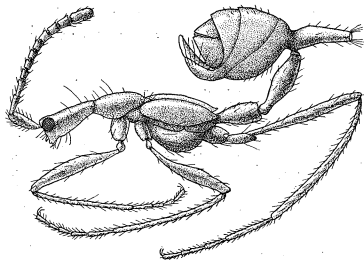


Fig. 4. — Lateral view of *Aemictoleras chapmani*, gen. et sp. nov

lobes long and narrow, each terminating in a tuft of long, curved hairs. Labial palpi 3-jointed, terminal joint slender and styliform, as long as the two basal stouter joints together. Prothorax narrower and smaller than the head, more than one and a half times as long as broad, its sides subparallel behind, its posterior border straight, its anterior half with rounded sides, narrowed and converging to the occipital articulation. Mesosternum very short; mesocoxae separated; metasterna large, convex, ovoidal, conspicuously projecting. Scutellum well-developed, triangular; elytra narrow, convex, together broader than the prothorax, their tips prolonged, acuminate and rather blunt. Wings well-developed, compactly folded under the elytra. First and second abdominal segments long and narrow, subfusiform, constricted anteriorly, the first shorter and stouter than the second; remainder of abdomen forming a somewhat lenticular, laterally compressed mass, the third segment prolonged ventrally as a long tubular structure, somewhat curved near the middle, constricted at the base and truncate at the tip, which

bears a circlet of hairs surrounding what seems to be the opening of a gland. Fourth and fifth segments each prolonged dorsally as a curved, convex scale, that of the fourth segment shorter and closely applied to the one on the fifth segment. Remaining segments short, together forming a flattened, cleft cone, terminating in the anus. In all the specimens the abdomen is curled dorsally, so that the ventral tube of the third segment points backward and the scale-like dorsal projections of the fourth and fifth segment point forward. Legs long and slender; tarsi 4-5-5-jointed; coxae large, dentate at their apices; hind trochanters large, their ventral apices prolonged and lobate; hind basitarsus as long as the two succeeding joints together; tarsal claws slender and rather straight.

Genotype : *Aenictoteras chapmani*, sp. nov.

Aenictoteras chapmani, sp. nov.

(Figs. 1 and 2).

Length nearly 3 mm. Castaneous brown; antennae, legs including coxae, first and second abdominal segments, base of third and dorsal process of fourth, paler and more reddish. Surface of body smooth and shining, with sparse piligerous punctures; antennae subopaque; prothorax, legs, anterior portion of first abdominal segment and surfaces of the scale-like dorsal processes of the fourth and fifth segments coriaceous or finely punctate-rugulose; sides and posterior portion of the prothorax more sparsely, metepisterna more coarsely and densely punctate. Hairs on the body erect, sparse and delicate, of uneven length, on the legs more numerous and oblique. Antennae with conspicuous hairs at the distal ends of the several joints.

Described from three specimens taken by Dr. J. W. CHAPMAN, April 6, 1924, at Dumaguete, Negros Oriental, Philippines. Each was being carried by a migrating worker of *Aenictus* (*Typhlatta*) *martini* Forel.

This strange beetle may be said to resemble the worker of its host ant, and the late Father E. WASMANN, S. J. would certainly have hailed it as another of the remarkable examples of myrmecophile mimicry, which he never tired of describing and illustrating. Though smaller, the *Aenictoteras* is, indeed, much like its host in color, sculpture and pilosity, and in the body and legs, but on closer scrutiny the form of the head, thorax and upwardly curved abdomen is very different. There is certainly nothing ant-like about the head, the conspicuous swelling of the metasterna and the first and second abdominal segments, which are far too long and slender to simulate a Doryline pedicel. And though the remaining abdominal segments form a mass analogous to the ant's gaster, they are laterally compressed and their large tubular and scale-like processes are quite unlike any structures in ants. The thin white membrane covering the truncated end of the tubular process on the third segment seems to represent the opening of a duct from some

gland, either repugnatorial or alluring, situated in the third segment, and the articulations of this and the two basal segments are so mobile as to suggest that in life the dorsally curved « gaster » can be moved about in such a manner as to permit the ventral tube of the third segment to be pointed, like a gun, in almost any direction. The significance of the narrow dorsal scale-like processes of the fourth and fifth segments is obscure, but they seem to be the homologues of the two prominent tubercles in the mid-dorsal region of the same segments of the Myrmedoniine genus *Nototaphra* Casey (sometimes included in the genus *Myrmedonia*), which comprises two spe-

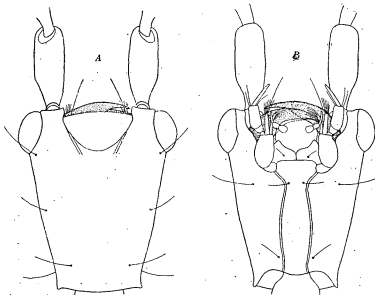


Fig. 2. — A, dorsal; B, ventral view of head of *Aenictoteras chapmani*, gen. et sp. nov.

cies, *lauta* Casey and *lugubris* Casey, both guests of our common North American *Tapinoma sessile* Say.

The considerable number of supposedly mimetic Aleocharine *Staphylinidae*, occurring mainly with species of *Eciton* (sens. lat.) in the New; and with *Dorylus* (sens. lat.) in the Old World, may be divided into three groups:

1. Forms departing from the usual Staphylinid type in having the head and thorax narrowed, the legs long and the abdomen constricted at the base. In these cases we may admit a certain superficial mimetic resemblance to the hosts in form and frequently also in color and sculpture. Here belong a number of ecitophiles of the genera *Ecitophya*, *Ecitophytes*, *Ecitomorpha*, *Mimeciton*, *Ecitophanes*, *Pulicomorpha*, *Mimonilla*, *Acamatoxenus*, *Acamatusina*, *Leptanillophilus*, *Ecitogaster*, *Labidominus* and *Ecitonilla*, and a smaller number of dorylophiles of the genera *Dorylo-*

stethus, *Doryiomimus*, *Dorylogaster*, *Dorylonia*, *Dorylocrates* and *Dromanomma*.

2. In three genera of ecitophiles, namely, *Ecitocryptus*, *Cryptomimus* and *Diploeiton*, the two basal abdominal segments are greatly narrowed and more or less nodiform so that they resemble the petiole and postpetiole of their hosts, while the remaining segments form together an ellipsoidal « gaster ». In these cases, the mimicry may be said to be decidedly more striking.

3. In three other genera, namely, the ecitophile *Chrematoxenus*, the dorylophile *Mimanomma* and the aenictophile *Aenictoteras* above described, the two basal abdominal segments are much more cylindrical or elongated, so that the pedicel is quite unlike that of the host-ant. *Aenictoteras* most closely resembles *Chrematoxenus aenigma* Mann, in which only the second abdominal segment is considerably elongated; in *Mimanomma spectrum* Wasm. it is the first segment which is elongated. Moreover, the thorax and head of this remarkable insect are also long and cylindrical, so that its resemblance to a *Dorylus* (*Anomma*) worker, even in profile, seems to me to be very remote, though it greatly impressed WASMANN. To regard the beetles of the three genera above mentioned as so many cases of hypertely really explains nothing, for why should they have developed beyond the much more mimetic stage of such forms as *Ecitocryptus* and *Ecitomimus*?

The ant-like appearance of the *Aenictoteras* above described is interesting in connection with the rather acrimonious discussion on mimicry carried on for several years between HEIKERTINGER on the one hand and WASMANN and REICHENSPERGER on the other. The perusal of their contributions shows that both parties failed signally in emphasizing their ignorance of certain essential facts about which no one in fact possesses any knowledge, namely the actual life history and detailed behavior of any single one of the numerous described species of supposedly mimetic Aleocharine ecitophiles and dorylophiles. All of these insects are known only from dried or alcoholic specimens which have been picked up by various collectors either from the migrant columns or the bivouacking agglomerations of their host-ants. HEIKERTINGER is certainly to be commended for his attempts to destroy the great fabric of often fanciful and fictitious conjecture which WASMANN has been weaving for so many years in his monastic reclusion. At the same time it must be admitted that HEIKERTINGER was at a disadvantage in not possessing WASMANN's and REICHENSPERGER's intimate knowledge of the actual specimens.

I believe that any unprejudiced entomologist who has examined extensive collections of these beetles, or who has taken them in their native environments, will agree that some of the species exhibit startling superficial resemblances in form, sculpture, pilosity and color to the hosts among which they live. He will be convinced, however, that until we have more definite knowledge of the beetles and the reactions of their hosts, specula-

tions like those in which WASMANN indulged, merely confuse the whole matter. Without entering into a long discussion, I would here call attention to a few considerations which have been either slurred over or distorted in the turmoil of the WASMANN-HEIKERTINGER polemics.

1. It is well known that all the workers of Doryline ants belonging to the genera *Dorylus* (sens. lat.), *Aenictus* and *Cheliomyrmex* are eyeless and therefore totally blind. This is true also of a number of species of *Eciton*, especially of the subterranean forms of the subgenera *Labidus* and *Acamatus*, but many species of *Eciton* (sens. str.) and *Acamatus*, which carry on their forays above ground, possess a pair of small lateral ocelli, which often have a hemispherical cornea but lack pigment. Since it happens that most of the mimetic Aleocharines have been taken with these ocellate Ecitons, WASMANN has repeatedly commented on their visual powers. He states positively that the ocelli are not vestiges of the compound eyes so generally present in the non-doryline ants, but phylogenetically new acquisitions (« Neuerwerbungen ») and that they enable their possessors to distinguish the form and color of their Aleocharine guests. There is not the slightest evidence, however, for either of these assumptions. According to the simplest and most natural hypothesis, the lateral ocelli are greatly reduced remnants of ancient compound eyes, a view commonly held also in regard to the lateral ocelli of Lepidopteran and Tenthredinoid larvae. Concerning their powers as visual organs no statement can be made till they have been experimentally investigated. But the brief study of their structure in *Eciton* (*Acamatus*) *schmitti* Emery, which I published as long ago as 1902 (p. 188, *nota*), and which is here quoted because it was ignored by WASMANN, shows that the actual conditions are very far from supporting his assumption: « I have recently sectioned a number of pupae of *Eciton schmitti* and find that the ocelliform lateral eyes are really much atrophied compound eyes, too much atrophied, in fact, to be at all functional as visual organs. The retinal hypodermis which is somewhat thickened under the convex lens [cornea], shows indistinct but unmistakable traces of ommatidia. The optic nerve is very short and not connected with the brain. It ends freely in a blunt point a short distance from the ommatidial layer. This is interesting as proving that the visual fibres must arise in the retina and grow towards the brain and not in the reverse direction from cells in that portion of the brain known as the optic ganglion. If there is a distinction between the abortive eyes of the *Dorylinae* and *Ponerinae* it would seem to be that in the former subfamily the ommatidia disappear both by fusion with one another and by reduction in number, while in the latter the number of ommatidia is gradually reduced without fusion. » If future investigation shows that the lateral ocelli of the large Ecitons (*E. hamatum*, *burchelli*, *praedator*, etc.) have the same structure as those of *E. schmitti* — and this is highly probable

from external examination — we should have to conclude that all the species of the genus are as blind as the species of *Dorylus* and *Aenictus*. We have, therefore, at the present time no evidence of vision in the workers of any of the Doryline ants ⁽¹⁾.

2. Although there is no evidence that any Doryline ants can see the guests which accompany them on their forays and migrations, the mimicry enthusiast may assert, nevertheless, that the *Eciton*-like appearance and coloration of the guests serve to protect them from the attack of insectivorous birds and mammals. This would have weight if it could be proved that the Doryline ants are immune to the attacks of such predators, but the facts by no means support the contention. There are certain birds, in both the Ethiopian and Neotropical Regions, that habitually follow the foraging columns of the Doryline ants, and while they may feed largely on the miscellaneous insects flushed by the foragers, there is considerable evidence that the ants are also devoured. BEQUAERT (1922) in a careful review of the literature has shown that the stomachs of birds of the African genera *Alethe*, *Bleda* and *Neocossyphus*, which habitually follow the columns of *Dorylus* (*Anomma*), not infrequently contain these ants. Moreover, certain African mammals, especially the elephant shrews, are also known to feed on *Dorylus*. Mr. Arthur LOVERIDGE informs me that *Rhinonax petersi* has this habit in Tanganyika Territory, and that in the same region he found the stomach of a *Petrodromus sultan* filled with workers of *Dorylus* (*Anomma*) *nigricans*. Flocks of « ant-thrushes » (*Formicariæ*) regularly follow the foraging columns of the large epigaeic *Ecitons* (*E. hamatum*, *burchelli*, *rapax*, etc.) in the American tropics. It is usually stated that they feed only on the insects flushed by the ants, but this must remain an assumption till the stomach-contents of these birds have been investigated. BEQUAERT (1930) has recently found in the literature some very definite observations by LUND (1831) on the preying of several South American birds (*Dendrocolaptes*, *Tanagra*, *Drymophila* and *Lanius*) on *Eciton*. It seems rather improbable, therefore, that the mimetic resemblances of the *Aleocharinae* to their hosts have arisen as a means of protecting them from predaceous birds and mammals. Indeed, it seems probable that the worker *Ecitons* would be devoured by the birds more readily than the large soldiers with their fish-hook-shaped mandibles, and since the *Aleocharines* resemble the minor workers they would actually be in danger of being as readily devoured. We seem to be left, therefore, without any explanation of the color resemblance of the mimetic dorylophiles and ecitophiles to their hosts.

(1) It is not improbable that the general hypodermis of the heads of the soldier *Ecitons* is photoreceptive, or capable of discriminating between light and darkness. This is indicated by the lack or small amount of pigment in the entire cephalic integument of the soldiers of such species as *E. hamatum* and *burchelli*. In other species (*E. praedator*) the head of the soldier or larger worker is paler than in the smaller individuals. Probably, also, the pale, pigmentless spots on the posterior corners of the head in all workers of the epigaeic *Aenicti* of the subgenus *Typhlatia* (*Ae. martini*, *laeviceps*, etc.) have a similar, photoreceptive function.

3. In order to account for the form and sculpture resemblances of the Aleocharine guests to their hosts we may, perhaps, have to resort to WASMANN's hypothesis of tactile mimicry. This conception, however, has been needlessly complicated and vitiated by his assumption that the ants are not deceived by the beetles, but are aware of their alien character. He has not informed us how he obtained this insight into the immediate sensory experience of the *Dorylinae* but seems merely to have extended certain inferences from his studies of European ants to ants with very different habits. And although he cites (1904) as support some observations of Father KOHL in the Belgian Congo, their perusal shows them to have been very casual and incomplete. We know that the guests in the marching armies of the *Dorylinae* are utterly ignored by their hosts, except in very rare instances, such as *Aenictoleras*, which, according to CHAPMAN, is actually carried by the ants. WASMANN, who never saw living *Dorylinae*, seems to have imagined that they spend their lives foraging. On the contrary, most of their lives is spent in their bivouacks, or temporary nests under logs or stones, in hollow tree-trunks or in cavities in the soil. In these retreats they often remain for weeks or months in dense agglomerations, especially while they are hibernating, estivating or bringing up their brood. We must suppose, therefore, that the guests have acquired the adaptive and mimetic peculiarities, which WASMANN has endeavored to explain, under these conditions, which must keep the guests in very close contact with the bodies of the ants, their brood and the prey which they have collected. This dark and crowded environment is pervaded with the powerful fecal stench so characteristic of all the *Dorylinae*. Hence, many of the peculiarities of the mimetic *Aleocharinae* may be adaptations to the singular nesting behavior of their hosts and to the unusual physical and chemical environment in which this behavior is manifested. Instead, therefore, of excogitating conjectures from preserved specimens, we should turn to precise observation and experimental investigation of the living *Dorylinae* and their guests at some of the biological stations that are being established in the tropics. For such purposes the Barro Colorado Laboratory in the Panama Canal Zone would seem to offer unusual opportunities owing to the confinement of several large species of *Eciton* to a small island.

LITTERATURE.

- BEQUAERT (J. C.). 1922. — The Predaceous Enemies of Ants. In WHEELER, Ants of the Belgian Congo. (*Bull. Amer. Mus. Nat. Hist.* 45 : 271-332, 2 pls.).
- BEQUAERT (J. C.). 1930. — Are Ants better protected against the attacks of their predaceous enemies than other Arthropods? (*Zool. Anzeig.* 88 : 163-176).
- BORGMEIER (T.). 1930. — Zwei neue Gattungen ecitophiler Aleocharinen. (*Zool. Anzeig.* 92 : 165-178, 27 figs.).
- BRUES (C. T.). 1904. — On the relations of certain myrmecophiles to their host-ants. (*Psyche* 11, pp. 21, 22).
- BRUES (C. T.). 1930. — *Acnictomyia*, a new myrmecophilous Phorid from the Philippines. (*Psyche*, 37 : 163-166, 1 fig.).
- FENYES (A.). 1918-1921. — Family *Staphylinidae*. Subfamily *Aleocharinae*, in *Genera Insectorum*. Fasc. 173 a-c.
- HEIKERTINGER (F.). 1919. — Die metöke Myrmekoidie (*Biol. Zentralbl.* 39 : 65-102, 13 figs.).
- HEIKERTINGER (F.). 1925. — Ueber die Begriffe « Mimikry » und « Mimese ». (*Biol. Zentralbl.* 45 : 272-289).
- HEIKERTINGER (F.). 1925-1927. — Die Ameisenmimese. I, Die Gesichtsmimese. (*Biol. Zentralbl.* 45, 1925, pp. 705-729, 4 figs.). II, Die « gesetzmässige » Färbungsübereinstimmung zwischen Gast und Wirt. (*Ibid.* 46, 1926, pp. 351-382, 385-405, 5 figs.). III, Die Tastmimese. (*Ibid.* 46, 1926, pp. 593-625, 4 figs.). IV, Die Lösung des Problems. (*Ibid.* 47; 1927, pp. 462-501, 47 figs.).
- HEIKERTINGER (F.). 1927. — Ueber Föhlreranpassungen bei myrmekophilen Käfern. (*Zeitsch. wiss. Insektenbiol.* 22 : 124-147).
- MANN (W. M.). 1921. — Three new Myrmecophilous Beetles. (*Proc. U. S. Nat. Mus.* 59 : 547-552, 6 figs.).
- MANN (W. M.). 1922. — Notes on a Collection of West African Myrmecophiles. In WHEELER, Ants of the Belgian Congo (*Bull. Amer. Mus. Nat. Hist.* 45 : 623-630, 2 figs.).
- MANN (W. M.). 1924. — Myrmecophiles from the Western United States and Lower California. (*Ann. Ent. Soc. Amer.* 17 : 87-95, 2 figs.).
- MANN (W. M.). 1926. — New Neotropical Myrmecophiles. (*Journ. Washington Acad. Sc.* 16 : 448-455, 1 fig.).
- REICHENSPERGER (A.). 1925. — « Ameisenmimikry » und « Metöke Myrmekoidie ». (*Biol. Zentralbl.* 45 : 290-303, 1 fig.).
- REICHENSPERGER (A.). 1926. — *Cryptomimus*, eine neue myrmekoide Staphylinidengattung. Zugleich eine Antwort an Herrn Heikertinger (*Zool. Anzeig.* 69 : 113-155, 1 fig.).
- REICHENSPERGER (A.). 1929. — Systematische und ökologische Myrmekophilen-Beiträge. (*Zool. Anzeig.* 82 (Wasmann-Festband), 257-268, 5 figs.).
- WASMANN (E.). 1904. — Zur Kenntnis der Gäste der Treiberameisen und ihrer Wirte am oberen Kongo, nach den Sammlungen und Beobachtungen von P. H. Kohl bearbeitet. (*Zool. Jahrb.*, Supplem. VII (Festschrift f. A. Weissman) : 611-682, 3 pls.).
- WASMANN (E.). 1912. — *Mimanomma spectrum*, ein neuer Dorylinengast des extremsten Mimikrytypus. (*Zool. Anzeig.* 39 : 473-181, 8 figs.).
- WASMANN (E.). 1915. — Revision der Gattung *Aenictonia* Wasm. (*Ent. Mitteil.* 4 : 26-35, 1 pl.).
- WASMANN (E.). 1915. — Erster Nachtrag zur Revision der Gattung *Aenictonia* Wasm., nebst einer Revision der Gattung *Dorylonia* Wasm. (*Ent. Mitteil.* 4 : 202-288).

- WASMANN (E.). 1915. — Zweiter Nachtrag zur Revision der Gattung *Aenictonia* Wasm. (*Ent. Mitteil.* 4 : 289-290).
- WASMANN (E.). 1917. — Neue Anpassungstypen bei Dorylinengästen Afrikas. (*Zeitschr. wiss. Zool.* 117 : 257-360, 3 pls.).
- WASMANN (E.). 1925. — Die Ameisenmimikry. Ein exakter Beitrag zum Mimikryproblem und zur Theorie der Anpassung. In SCHAXEL's *Abhandl. Theoret. Biol.*, Heft 19, 164 pp., 3 pls.).
- WASMANN (E.). 1926. — Zur Streitfrage der Ameisenmimikry. (*Zool. Anzeig.* 68 : 273-282).
- WASMANN (E.). 1928. — Zur Kenntnis von *Mimeciton* und der Anpassungen der Myrmecophilen. Eine Antwort an Franz Heikertinger und W. M. Wheeler. (*Zool. Anzeig.*, 76 : 165-184, 11 figs.).
- WHEELER (W. M.). 1902. — An American *Cerapachys*, with remarks on the affinities of the *Cerapachyinae* (*Biol. Bull.* 3 : 181-191, 5 figs.).